

Decomposition of wood

Afbraak van hout

A. Käärik

Swedish University of Agricultural Sciences, Department of Forest Products, Uppsala (Sweden)

1 Introduction

The decomposition of wood is a long and complicated process with many biotic and abiotic factors involved. This process begins with the establishment of micro-organisms and decay fungi in unprotected woody tissues, as in wounds of living or on debarked wood surfaces of dead trees and ends with the total decomposition of the wood.

Ecological investigations concerning the whole decay process and its relation to the environmental factors are few. To get a picture on the decay process of wood in different situations we have to draw from existing investigations on the separate phases of decay in various wood species, from floristic studies as well as from laboratory studies on the decay processes and factors which influence them.

2 Bark, its properties and decomposition

The wood of both living and dead trees is efficiently protected by the thick, highly suberized layers of the outer bark. Only a few micro-organisms are able to penetrate the thin periderm layers on small branches. On the average, bark comprises 9-15% of a trunk volume or 13-21% of its dry weight (Harkin & Rowe 1971). The protective action of the bark is caused by its structure and its chemical properties, especially by the high content of bark lignins and extractives, which may inhibit the growth of micro-organisms.

The bark of *Pinus sylvestris* and *Picea abies* contains 50-60% carbohydrates, mainly cellulose, 30-40% lignin and 2-3% suberin. It has a relatively high Ca and very low N and P content (Olsson 1978). Chemically, bark lignin differs considerably from wood lignin by its poorer solubility and its higher heterogeneity.

Due to its chemical composition, degradation of bark is a slow process. Under natural conditions, the dry weight loss of beech bark is about 30-40% after two years and that of spruce bark about 60% (Wilhelm 1975). Similarly, under field conditions, the weight loss of outer bark of Scots pine is only 5% after 15 months and that of the inner bark, richer in nutrients, is 32%

Samenvatting

Het ingewikkelde proces van afbraak van dode bast en dood hout staat onder invloed van biotische en abiotische factoren. De chemische achtergrond van beide processen wordt behandeld, waarbij de bast veel moeilijker blijkt te verteren en veel bestendiger afbraakprodukten oplevert dan hout. Een inventaris van houtbewonende bacteriën en schimmels en hun afbraakactiviteiten wordt gegeven: de stikstofbindende bacteriën die erbij zijn verdienen aandacht. Verschillende schimmels houden zich bezig met verschillende delen van dode cellen en vezels. De invloed van abiotische factoren (vocht, temperatuur, zuurgraad, koolzuur, stikstof) wordt besproken, en de weerstand van hout. Dit wordt vertaald naar de bossituaties, van stervende bomen tot dood hout en van verschillende naaldboomsoorten tot loofboomsoorten. In dikke en dunne gevallen stammen, in stobben en in takken, treden telkens verschillende processen op. De vaak gestelde associatie van "wit rot" met dood hout van loofbomen en van "bruij rot" met dood hout van naaldbomen blijkt niet zo simpel te liggen: op dood hout van naaldbomen in de natuur zijn beide categorieën schimmels actief. Vergeleken met oerbos is het aantal houtrotschimmels laag in cultuurbos. Veel van de bruinrotschimmels verschijnen pas laat in de successie, omdat ze stammen met veel kernhout nodig hebben. Bruinrotschimmels zijn echter juist van veel belang, omdat ze stabiele humus produceren en de plaats zijn voor stikstoffixatie.

(Olsson 1978).

Isolations of decay fungi from naturally decayed bark have failed, but a number of moulds and soft rot fungi have been isolated (Caldwell 1963, Kuhlman 1969, Wilhelm 1975). Under laboratory conditions these fungi are able to cause a rather high dry weight loss of about 3-6% after 12 weeks. At the same time the dry weight loss caused by white rot fungi was 6-8% and by a brown rot fungus 12%. After 12-15 weeks the degradation of bark comes practically to a standstill (Kuhlman 1970).

During the bark decomposition process intermediate products are formed which become condensed and polymerized to high molecular and relatively stable humus substances which are not easily used by fungi. Some brown rot fungi can only grow on fresh bark, using non-degraded bark compounds, whereas some white rot fungi can also attack partly humified barks, further degrading cellulose and lignin decomposition products and producing fulvin-acid like substances (Jodice et al. 1979).

Thus, the bark may be attacked with difficulty by the common wood decay fungi. The decomposition process, especially of the relatively nutrient-rich inner bark is rather rapid during the first 2-3 months. After the depletion of easily metabolized nutrients the decomposition process slows down or comes to a standstill, as most bark constituents, due to their complex structure, are resistant to the enzymatic breakdown by decay fungi.

3 Wood, its structure and chemistry

Woody tissues are characterized by their high content of lignocellulosic material. The main components of some wood species are as follows. Pine: content of lignin 28.1%; pentosans 9.4%; cellulose 61.0%. Spruce: lignin 27.1%; pentosans 8.5%; cellulose 63.6%. Birch: lignin 19.6%; pentosans 27.2%; cellulose 52.4% (Henningsson 1962). Angiosperm wood is distinguished by its high content of pentosans and gymnosperm wood by its high content of hexosans and lignin. The main non-glucose sugar in angiosperm wood is xylan and in gymnosperm wood mannose. Several mono-, di-, and oligosaccharides also occur in non-polymerized form. Cellulose is composed of d-glucanopyranose units linked by 1,4- β glucosidic bonds into linear molecules of a very high degree of polymerization. In woody cell walls cellulose exists partly in crystalline, partly in paracrystalline form, built up as microfibrils and elementary fibrils. The space between the fibrils is filled with hemicelluloses, lignin and varying amounts of water (Bailey et al. 1968). The hemicelluloses of wood have a much lower degree of polymerization and a non-crystalline form. Lignin is a complex 3-dimensional natural polymer, containing many types of chemical linkages between its phenylpropanoid units (Kirk & Harkin 1973). There is an intimate relationship between the cellulose, hemicellulose and lignin components of the wood and their degradation in nature is a complex process.

4 Woodinhabiting micro-organisms and their action on wood

4.1 Bacteria

a Wood inhabiting and wood degrading bacteria

Bacteria are among the first colonizers of wood in a moist situation. They accumulate in ray parenchyma and are living on readily soluble cell contents. Under certain conditions, as in wood that has been exposed a long time to constant high moisture content, bacterial attack on cell walls may occur (Harmsen & Nissen 1965, Boutelje & Bravery 1968). Some of the bacteria may influence the attack of decay fungi by inhibiting or stimulating their decay capacity (Henningsson 1967, Greaves 1970).

b Nitrogen fixing bacteria

The presence of nitrogenase activity in decayed wood has been known for some years (Cornaby & Waide 1973, Sharp & Millbank 1973). The presence of bacteria in decaying wood capable of fixing nitrogen has been reported by Seidler et al. (1972) and Aho et al. (1974). Larsen et al. (1978) showed that nitrogenase activity coexists naturally with decay fungi in woody substrates and that advanced brown-rotted wood is the most favourable substrate for such activity. They calculated a nitrogen fixation of 735 g/ha by woody residues during 100 days in their experimental forest. Thus, the decaying woody residues are important components of the nitrogen cycle and they therefore have an important biological function.

4.2 Fungi

a Degrading no woody cell walls but largely exhausting dead cell contents: moulds and blue stain fungi

These fungi belong to the very early and to the late colonizers of decaying wood. They mainly feed on dead cell contents, on intermediate metabolites of higher fungi and on desintegrating cells of other organisms. They are found among Phycomycetes, Ascomycetes and Fungi Imperfecti. Most of the moulds are common organisms in forest soil (Widden & Parkinson 1978). A strong amylase, xylanase, pectinase and also cellulase activity characterizes these fungi (Wolf & Liese 1977), which in severe attack may destroy the non-lignified cell walls. A number of the moulds may interact with decay fungi by inhibiting or stimulating them (Shigo 1965, Singh & Tewari 1970, v. Aufsess 1976). Blue stain fungi cause discoloration of wood due to their pigmented hyphae. In above-ground conditions they penetrate wood deeper and more rapidly than the moulds. They are able to enzymatically decompose cellulose derivatives but not the unaltered native cellulose. In decomposing wood they disappear after a relatively short time, before the attack of decay fungi reaches its

optimal phase (Käärik 1975).

b Fungi with a limited degradation capability: the soft rot fungi

These fungi grow in the S_2 layer within the secondary cell wall (Fig. 1) and enzymatically dissolve the wall substance to form cavities that are oriented either helioidally around or parallel to the long axis of the cells. Most of these fungi also are common organisms in forest soils (Widden & Parkinson 1973), and they may be pioneers of newly exposed wood. Soft rot type of attack resembles that of brown rot in that principally the carbohydrates are attacked and lignin is attacked or modified to a lesser extent by a demethoxylation process (Seifert 1966). The ease with which the soft rot rotters attack hardwoods may be related to the availability of the xylan in their cell walls (Levy 1973).

c Fungi enzymatically degrading cellulose and hemicelluloses of the cell wall: the brown rot fungi

Wood attacked by brown rot fungi has a brown shrunken cubical appearance. Brown rot is caused by Basidiomycetes which utilize the hemicelluloses and cellulose of the cell wall, leaving the lignin essentially undigested. Lignin is, however, modified by demethylation and in decayed wood oxidized polymeric lignin degradation products are accumulated. (Kirk & Adler 1970, Kirk 1975). Hyphae of brown rot fungi grow in cell lumina in close contact with the S_3 layer. The secreted enzymes affect the S_2 layer in a diffuse manner over the whole cell wall (Fig. 2), where the polysaccharides are broken down (Necessary 1963). The residual lignin maintains the shape of the cell wall so that little damage is apparent until late stages when the whole residual cell wall collapses.

The brown rot fungi damage the wood structure by rapidly depolymerizing the cellulose at the initial stages of decay before any substantial loss of the total dry weight takes place. At this stage cellulose is depolymerized much faster than the breakdown products can be metabolized (Cowling 1961). During the next phase of decay a gradual weight loss and a much slower depolymerization of both cellulose and hemicelluloses occurs the lignin complex is also attacked at that stage. Thoroughly brown-rotted wood is mainly partly degraded lignin.

d Fungi degrading both cellulose and lignin of the woody cell wall: the white rot fungi

A bleached appearance is characteristic of white rot. Fungi causing white rot are distinguished by enzymes capable of degrading both cellulose, hemicelluloses

and lignin and they belong mainly to Basidiomycetes. The cell wall layers are attacked from the cell lumen outward, thus producing a gradual thinning of the cell wall (Liese 1965). In white rot fungi with weaker enzymatic activity the attack is restricted to the S_3 layer (Ravilly & Dirol 1977). Some of the white rot fungi decompose the cell wall successively, beginning with the lignin and hemicelluloses and deteriorating cellulose at a later stage; this type of attack is often found in coniferous wood. Other fungi simultaneously decompose all substances of the cell wall; such fungi preferentially attack hardwood. When cellulose is attacked, it is degraded at about the same rate at which the breakdown can be metabolized (Cowling 1961). White rot fungi possess a lignin metabolizing enzyme that is lacking in brown rot fungi. However, hitherto not a single enzyme involved in lignin degradation has been identified. Kirk (1975) emphasizes that there is a parallel effect of white and brown rot fungi on lignin, but the lignin-degrading capacity of the brown-rot fungi is incomplete.

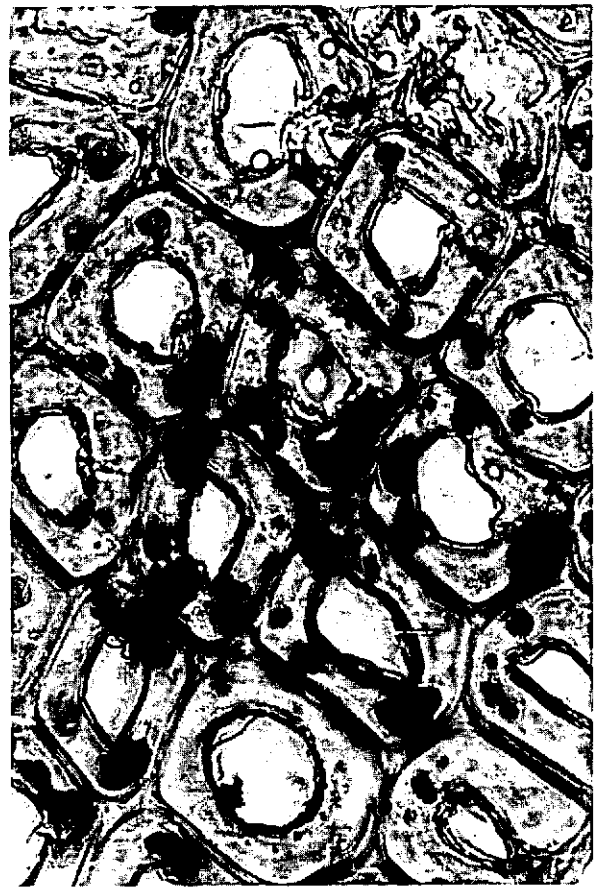


Fig. 1 Heavy attack of soft rot in the secondary cell wall of *Pinus sylvestris* tracheids. Polarized light, $\times 600$.

5 Ecology of wood-destroying micro-organisms

5.1 Factors influencing decay

Climatic and nutritional factors influence the growth and decay activity as well as different interactions between the various fungi. They thus have a marked influence on the associations and successions of fungi colonizing wood in different situations.

a Moisture content of the wood has to be above the fibre saturation point, i.e. above 24-31% of dry weight before any blue stain or decay fungi can attack the wood. The optimal and maximum values are very variable. Wood with a moisture content of 60-100% decays rapidly; 120% may be the limit for some decay fungi; but optimum values between 160-180% have been found for others. For soft rot fungi the optimum values may be as high as 200-240% (Liese & Ammer 1964). Light-weight wood absorbs more water than denser wood and is thus more susceptible to fungus activity, but as it also dries more rapidly, deterioration might be retarded and stopped earlier in such wood (Courtois 1968).

b Temperature. The wood-destroying fungi rank among eurythermal organisms with a wide temperature tolerance. Their optimum temperature varies between 20° and 32 °C. The lethal temperatures which depend on the moisture content of the wood, and which may be 10-25 °C higher than the maximum temperature for growth, are of importance for their survival (Kurpik & Wazny 1978).

c pH. Tolerance of wide ranges of pH, between 4.0 and 9.0 and an optimum between 5.0-6.0 is common among wood-inhabiting fungi (Butcher 1968). The brown rot fungi tolerate lower and are more sensitive to higher pH values (Henningsson 1967a); tolerance of acidity is also greater in wood-inhabiting than in litter-decomposing Basidiomycetes (Hintikka 1969). During the action of wood-colonizing fungi, the pH of the wood usually becomes lower. The pH-changes are assumed to be an important factor affecting the competition of micro-organisms and influencing the rate of decomposition.

d Carbon dioxide content in dead coniferous wood is about 1.6% and in deciduous wood 3.5%, that is approximately 10-100 times as high as in the soil. Wood-inhabiting Basidiomycetes show a far greater tolerance to CO₂ than the litter-decomposing fungi (Hintikka & Korhonen 1970).

e The nitrogen content of mature wood is extremely

low, about 0.03-0.10% as compared to 1-5% for most herbaceous plants. The N-content of wood might be a limiting factor in decay; the dry weight loss has a direct and highly significant correlation to the nitrogen content of individual annual increments (Cowling 1970).

f Resistance of wood to decay. The sapwood of all wood species is susceptible to decay, but the rate of degradation is dependent on the wood species and the micro-organisms involved. The heartwood of some wood species may be more or less resistant to decay due to its extractives content. The heartwood of younger, second-growth trees is often less resistant than that of the more slowly grown virgin timber or trees grown on less productive sites (Scheffer & Cowling 1966).

The described complex of external factors acts selectively on the micro-organisms at the moment of infection and later on the successions of fungi.

5.2 Decay of wood in different situations. Successions and types of decay

a Living trees. Infection by decay fungi here occurs through wounds and is either preceded by, and dependent on a previous attack of non-decay organisms, as in the case of *Phellinus*-species, or the decay fungi are primary colonizers, as in the case of *Heterobasidion annosum*, *Chondrostereum purpureum* and *Inonotus tomentosus* (Shigo 1967).

On deciduous trees in Europe of the 35 important decay fungi, 30 are white and 5 brown rot fungi. The white rot fungi, especially *Phellinus* and *Inonotus* species, dominate in living deciduous wood. The question of the importance of brown rot fungi in conifers is rather interesting, as it is often postulated that the brown rotters are dominant on coniferous wood. On conifers in North and Central Europe of 18 more important fungi causing heart rot, 12 are white rot and 6 brown rot fungi (Cartwright & Findlay 1950). The greatest damages are caused by the white rotters *Heterobasidion annosum*, *Armillariella mellea*, *Phellinus pini* and *Stereum sanguinolentum*. The same situation is found in spruce stands in Norway and in Germany (Enerstvedt & Venn 1979, v. Pechmann & v. Aufsess 1971). Reports from Canada and USA confirm this relationship (Foster & Foster 1951, Hinds 1977). In the USA, in randomly selected stands of mixed conifers Hobbs & Partridge (1979) found 8 more important decay fungi, among which six white and two brown rotters. Locally, the brown rot fungus *Phaeolus schweinitzii* may dominate (Thomas & Thomas 1954, Courtois & Irslinger 1976). Thus, in Europe as in North America, in living conifers the main decay is caused by white rot fungi.

b In insect-attacked living conifers the first colonizers are blue stain and ambrosia fungi together with yeasts and bacteria. After some months, weakly parasitic or saprophytic white rot fungi follow, attacking the sapwood, and the blue stain fungi gradually decline. Brown rot fungi attacking heartwood appear in later stages of decay (Käärik 1975). In standing deteriorating trees the fungal successions are influenced especially by the strikingly decreasing moisture content of the wood. Deterioration rate may vary considerably: 25-28% of the volume of the trees after five years (Basham 1959) or 40% of the volume after 20 years (Hinds et al. 1965).

c On wind-felled coniferous trees the colonization also begins with the non-decay fungi, following by rapidly growing sapwood-attacking white rot fungi, such as *Stereum* and *Hirschioporus* spp.; these are later followed by brown rots such as *Fomitopsis pinicola* and *Gloeophyllum* spp. (Stillwell 1959, Engelhardt et al. 1961).

Jahn (1968) describes the whole fungus succession on deteriorating *Abies alba* boles according to sporophores found. The initial phase is characterized by a few Basidiomycetes; during the following optimum phase which can be as long as 10-30 years, numerous Polyporaceae and Stereaceae appear together with some Corticiaceae and Agaricaceae. The final phase with strongly decayed wood is characterized by numerous Agaricaceae. Of 19 fungi listed, two belonged to the brown rots.

d Stumps are initially colonized by non-decay fungi and the rapid white rot fungi. This initial phase varies from 0.5 to 5 years and is followed by the optimal phase with an attack of active white and brown rot fungi. At the final phase, after 5-7 years or more, numerous Agaricaceae, mostly of white rot type, appear (Käärik & Rennerfelt 1957, Meredith 1960, Jahn 1968, Runge 1978). The sapwood and heartwood of spruce shows a marked loss of density after four years; in pine stumps the picture is more complicated, because the content of resin substances increases, which impedes the decay (Käärik & Rennerfelt 1957). The stumps of deciduous trees are decomposed much more rapidly; their final phase begins already after 3,5-5,5 years (Runge 1978).

e Slash. The decomposition of dead branches and twigs of *Carpinus*, *Fagus* and *Quercus* in a mixed oak forest in Belgium has been analyzed by Ledel & Kestlemont (1975). The moisture content and also the dry weight loss of twigs and branches at the soil surface is essentially higher than at the crown height of felled trees. Dry weight loss at the soil surface after

one year is about 15-27% and at the crown height 10-22%. In the Northeast of the USA the average period for slash to disintegrate is 15 years for hardwoods, 17 years for *Pinus strobus* and 29 years for *Picea rubra*. Under most favourable conditions the decay period may be shortened by about one fifth (Spaulding & Hansborough 1944). The primary factors controlling decay in slash also are moisture, temperature and decay resistance of the wood. A short rotation time results in less slash per area unit and also in larger proportions of fast decaying sapwood. Even an open canopy maintains more uniform moisture and temperature conditions and group or selective cutting thus hastens the decay process. In clear-cuttings, the inner temperature in slash may be 40-55 °C under solar radiation at an air temperature of 31 °C (Loman 1962). These abnormally high temperatures and dryness greatly retard decay in both slash and stumps. A list of decay fungi on slash in mixed forest areas is given by Spaulding & Hansborough (1944). This list includes a number of common heartrot fungi of living trees, which are not only surviving on slash but are also of importance in slash decay. In such mixed forest areas, a high number of common angiosperm wood fungi also occur on gymnosperms and vice versa.

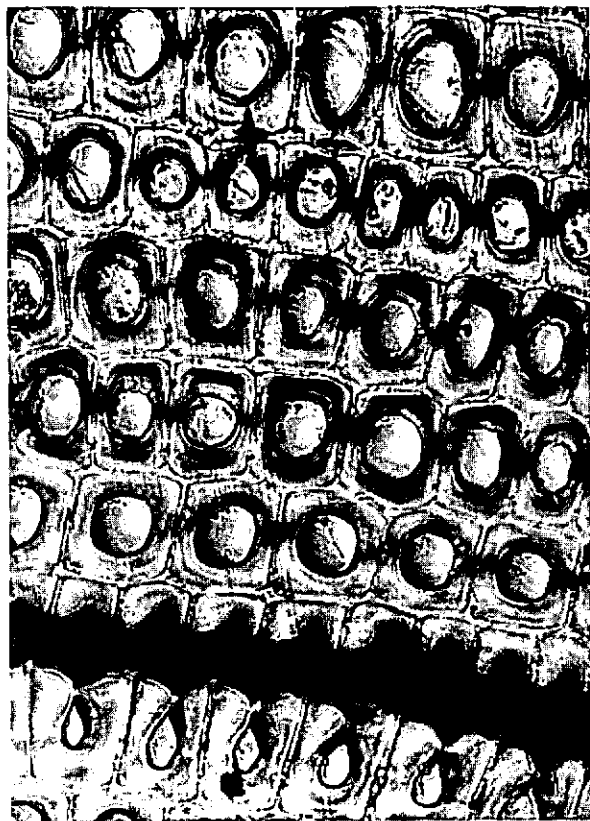


Fig. 2 Attack of brown rot in the secondary cell wall of *Pinus sylvestris* tracheids. Polarized light, $\times 480$.

f Decay of timber, logs and pulpwood. On unpeeled angiosperm logs Mangenot (1952) found marked successions of non-decay and decay fungi with white rot predominating. The same is true for *Fagus* logs in Japan (Ueyama 1965). In spruce logs the first colonizers are blue stain and mould fungi, followed by rapidly growing but less active and later by more active decay fungi (v. Pechman et al. 1967). In second-growth *Pseudotsuga* logs the decay amounts to 47% of the total volume after 6 years. White rots dominate at the initial stages with 68% of the total decay, but they decrease to 52% after 6 years. Brown rots increase at the same time from 16% to 30% (Smith et al. 1969). The moisture factor is of primary importance for the succession of fungi in decaying logs; the first colonizers are always fungi with a high tolerance to high humidity. The brown rot fungi, generally more tolerant to desiccation and also capable of attacking heartwood are more important in the later stages of decay in softwoods. Decay rates generally increase with decreasing log size and increasing percentage of sapwood (Smith et al. 1969). In principle, the same may be said of decay of pulpwood stored in the forest. In pine, birch and aspen pulpwood cellulose as well as lignins and pentosans are decomposed after 15 months by the action of common storage decay fungi and the decay is of the white rot type (Henningsson 1962).

6 Host-wood prevalence of the decay types

As the course of the breakdown process differs with white and brown rot fungi, just as the intermediate and final products of decay are different, so the relative role of the two decay types under natural conditions is of considerable importance. It is often maintained that in

above-ground situations white rot fungi are associated with decay of angiosperm and the brown rot with the decay of gymnosperm wood (Cowling 1961, Gilbertson 1981). The last assumption might not be valid under all circumstances, as the relationship of the decay fungi to their host wood is far more complicated. Table 1 gives some idea of the host-fungus relationship. It is based on data from Stalpers (1978) which refer to a selection of decay fungi from a global point of view, on data from Spaulding & Hansborough (1944), which refer to fungi on slash in a mixed forest area and on the data from Gilbertson (1981) which refer to analyses from northern coniferous forests. This table shows a rather good distribution of both groups of decay fungi to the main groups of host-wood, with a clear preference of white rot fungi to angiosperm wood. There are also large numbers of both brown and white rot fungi which may attack both angiosperm and gymnosperm wood. Gilbertson's (1981) data show that out of the North American brown rot fungi 50% only attack coniferous wood, but the other half also or only attacks deciduous wood. The question of the numbers of species preferring the different kinds of wood is not as important as the question as to which type of fungi is causing the main decay. On angiosperm wood the main decay from living trees to stumps and slash is caused by white rot fungi. Quite a number of brown rot fungi also belong to the angiosperm decay ecosystem but they are a minority. With brown rot fungi the situation is more complex. The degradation of coniferous wood in different situations is rather well studied and it is clearly seen, as cited on the above pages (item 5.2) that, from living trees to decaying stems, logs, stumps and slash, the main decay fungi causing the greatest volume losses are the white rot fungi. However, the brown

Table 1 The host-wood preference of some decay fungi. Numbers of species and percentage of total.

author, material examined	fungi examined	on gymnosperms		on angiosperms		on both	
		brown rot	white rot	brown rot	white rot	brown rot	white rot
Stalpers 1978, all kinds of wood	Polyporaceae	24	27	26	138	28	28
	Corticaceae	5	25	9	82	12	41
	Hydnaceae	—	4	—	7	—	4
	Coniophoraceae	2	—	—	—	2	—
	Totally 464 species % of total	31 6.8	56 12	35 7.5	227 49	42 9	73 16
Spaulding & Hansborough 1944 slash in mixed forests	Totally 70 species	5	6	1	12	19	27
	% of total	7	9	1	17	27	39
Gilbertson 1981	Only brown rot fungi	56		14		43	
	Totally 113 species % of total	50		12		36	

rot fungi clearly dominate on one kind of wood, and that is on conifer wood products, as on construction timber, buildings and often also on poles, sleepers and other wood products (Duncan & Lombard 1965). In these situations angiosperm wood is also attacked more often by brown rot fungi than normally (Duncan & Lombard l.c.). Differences in the type and amount of lignin between softwoods and hardwoods have been thought to be the factors governing the preference for hardwood by the white rot fungi (Petersen & Cowling 1964). It has been suggested that differences in the main hemicelluloses and their influence on enzymatic activity enable the brown rot fungi to compete better than the white rots on a softwood substrate (Highley, 1978). The prevalence of brown rot fungi mainly on a certain type of softwood indicates that the hostwood preference must be a multifactor effect, depending not only on the enzymatical differences of the white and brown rot fungi. In the northern hemisphere, both in mixed and coniferous forests, the white rot fungi are responsible for the main part of decay, but they work together with the brown rot fungi, one third to one half of the species of which is specialized on coniferous substrate; hence they play an essential role in the functioning of the coniferous forests ecosystems. According to Rypáček (1975) brown rot activity should be understood as a humification of the wood. During the decay by brown rot fungi, high molecular humic acids content is permanently increasing in decomposed wood at the cost of low molecular fulvic acids. During the decay by white rot fungi their ratio practically does not change. Brown rot residues are extremely stable and may persist in the upper layers of forest soils for a long time. The gradual decay process plays a key role in recycling nutrients and keeping them in the forest ecosystem (Gilbertson 1981). The brown rot residues are also a site for nitrogen fixation. Compared with virgin forests, the flora of decay fungi is strikingly poorer in the second-growth of well-cleaned forests. Many Polypores of the brown rot type appear late in successions; they require old decaying stems or slash of large dimensions and with a large part of heartwood. These fungi are the first to disappear in the second-growth forests with short rotations. There is a balance still existing between the white and brown rot fungi but we do not know in which direction alterations in the fungus flora may develop during long periods of time. Changes in this balance might influence the whole forest ecosystem.

Summary

The main types of micro-organisms colonizing and decomposing wood are described. The main types of de-

cay and their prevalence in nature from standing trees to slash are described.

Associations of white rot with deciduous wood and brown rot with coniferous wood are discussed. White rot is the dominating decay on deciduous wood. The brown rot fungi cause the main decay of coniferous forest products but on both living and dead conifers in nature the white rot and the brown rot fungi are equally responsible for the greatest part of the decay.

Literature

- Aho, P. E., R. J. Seidler, H. J. Evens & P. N. Raju. 1974. *Phytopathol.* 64: 1413-1420.
- Aufsess, H. von. 1976. *Material Organ.* 11 (3): 183-196.
- Basham, J. T. 1957. *Can. J. Bot.* 35: 155-172.
- Basham, J. T. 1959. *Can. J. Bot.* 37: 291-326.
- Basham, J. T. & R. M. Belyea. 1960. *Forest Sci.* 6: 78-96.
- Boutelje, J. B. & A. F. Bravery. 1968. *J. Inst. Wood Sci.* 20: 47-57.
- Butcher, J. A. 1968. *Can. J. Bot.* 46 (12): 1577-1589.
- Caldwell, R. 1963. *Trans. Brit. Myc. Soc.* 46: 249-261.
- Cartwright, K., St. G. & W. P. K. Findlay. 1950. *Decay of timber and its prevention.* - Chem. Publ. Co. Inc. N.Y. 294 pp.
- Cornaby, B. W. & J. B. Waide. 1973. *Plant Soil* 39: 445-448.
- Courtois, H. 1968. *Material Org.* 6 (1): 51-80.
- Courtois, H. & R. Irslinger. 1976. *Phytopathol. Z.* 86: 97-106.
- Cowling, E. B. 1961. *USDA For. Serv. Techn. Bull.* 1258: 79 pp.
- Cowling, E. B. 1970. *Acta Univ. Upsal. Diss. Sci.* 164.
- Duncan, C. G. 1960. *U.S. For. Prod. Lab. Madison Rep. No.* 2173, 26 pp.
- Duncan, C. G. & F. F. Lombard. 1965. *U.S. For. Serv. Res. Pap. WO-4*; 31 pp.
- Eaton, R. A. & E. B. Gareth Jones. 1971. *Material Org.* 6 (1): 51-80.
- Enerstvedt, L. I. & K. Venn. 1979. *Rep. Norw. For. Res. Inst.* 35 (4): 237-264.
- Engelhardt, N. T., R. E. Foster & H. M. Craig. 1961. *Studies in forest pathology XXIII.* - Canad. Dep. For. Ottawa, 20 pp.
- Etheridge, D. E. 1969. *Can. J. Bot.* 47 (3): 457-479.
- Foster, R. E. & A. T. Foster. 1951. *Can. J. Bot.* 29: 479-521.
- Gilbertson, R. L. 1981. *Mycotaxon* 12 (2): 372-416.
- Greaves, H. 1970. *Material Org.* 5: 265-279.
- Harkin, J. M. & J. W. Rowe. 1971. *USDA For. Serv. Res. Note FPL 091*; 53 pp.
- Harmsen, L. & T. V. Nissen. 1965. *Holz Roh-Werkst.* 23: 389-393.
- Henningsson, B. 1962. *Medd. Stat. Skogsforskningsinst.* 52 (3), 32 pp.
- Henningsson, B. 1967. *Stud. For. Suecica* 63, 31 pp.
- Henningsson, B. 1967a. *Stud. For. Suecica* 53.
- Highley, T. L. 1976. *Material Org.* 11 (1): 33-46.
- Highley, T. L. 1978. *Material Org.* 13 (3): 197-206.
- Highley, T. L. & T. K. Kirk. 1979. *Phytopathol.* 69 (10): 1151-1157.
- Hinds, T. E. 1971. *USDA For. Serv. Res. Rap. RM-65*, 11 pp.
- Hinds, T. E., F. G. Hawksworth & R. V. Davidson. 1965. *J. For.* 63 (7): 536-542.
- Hintikka, V. 1969. *Karstenia* 10: 177-183.
- Hintikka, V. & K. Korhonen. 1970. *Comm. Inst. For. Fenn.* 69 (5), 28 pp.

- Hobbs, S. D. & A. D. Patridge. 1979. *Forest Sci.* 25 (1): 31-42.
- Jahn, H. 1968. *Westfälische Pilzbriefe* 7 (2): 17-40.
- Jodice, R., N. Fiussello & J. C. Scurti. 1970. *Allionia* 16, 91-99. (*Boll. Inst. Orto Bot. Univ. Torino*).
- Kirk, T. C. 1975. In Liese, W. (Ed.) *Biological Transformation of Wood by Micro-organisms*. – 153-164.
- Kirk, T. C. & E. Adler. 1970. *Acta Chem. Scand.* 24: 3379-3390.
- Kirk, T. C. & J. M. Harkin. 1973. *Am. Inst. Chem. Eng. Symp. Ser. No. 133*, (69), 124-126.
- Kirk, T. K. & T. L. Highley. 1973. *Phytopathol.* 63 (11): 1338-1342.
- Kuhlman, E. G. 1969. *Can. J. Bot.* 47: 1719-1723.
- Kuhlman, E. G. 1970. *Can. J. Bot.* 48: 1787-1793.
- Kurpik, W. & J. Wazny. 1978. *Material Org.* 13 (1): 1-12.
- Käärik, A. 1975. In Liese, W. (Ed.) *Biological transformation of wood by micro-organisms*. – Berlin 1975, 39-51.
- Käärik, A. & E. Rennerfelt. 1957. *Medd. Stat. Skogsforskn. inst.* 47 (7), 88 pp.
- Larsen, M. J., M. F. Jurgensen & A. E. Harvey. 1978. *Can. J. For. Res.* 8: 341-345.
- Ledel, P. & P. Kestemont. 1976. *Bull. Soc. Roy. Bot. Belgique* 109: 259-273.
- Levy, J. F. 1973. *Brit. Wood. Preserv. Ass. News Sheet No. 130*, 2 pp.
- Liese, W. 1965. *Material Organ. Beih.* 1, 13-26.
- Liese, W. & U. Ammer. 1964. *Holzforsch.* 18 (4): 97-102.
- Loman, A. A. 1962. *Can. J. Bot.* 40: 1545-1559.
- Mangenot, F. 1952. *Reserches méthodiques sur les champignons de certain bois en décomposition*. – Paris, 115 pp.
- Meredith, D. S. 1960. *Ann. Bot.* 24 (93): 63-78.
- Necessany, V. 1963. *Holzforsch.* 17: 57-60.
- Olsson, M. T. 1978. *Rapp. Ecol. and For. Soils. Swedish Univ. Agric. Sci.* 34, 14 pp.
- Pechmann, H. von, H. von Aufsess, E. Liese & E. Ammer, 1967. *Forstwiss. Forsch. Beih. Forstwiss. Centralbl.* 27, 112 pp.
- Pechmann, H. von & H. von Aufsess. 1971. *Forstwiss. Centralbl.* 90 (4): 259-284.
- Peterson, C. A. & E. B. Cowling. 1964. *Phytopathol.* 54: 542-547.
- Ravilly, F. & D. Dirol. 1977. *Material Org.* 12 (1): 37-48.
- Runge, A. 1978. *Z. Mykol.* 44 (2): 295-301.
- Rypáček, W. 1975. *Wood Res. Proceedings* 20 (1): 1-22. Bratislava.
- Scheffer, T. C. & E. B. Cowling. 1966. *Ann. Rev. Phytopath.* 40: 147-170.
- Schmidt, O. & W. Liese. 1982. *Intern. J. Wood Preserv.* 2 (1): 13-19.
- Seidler, R. J., P. E. Aho, P. N. Raju & H. J. Evans. 1972. *J. Gen. Microbiol.* 73: 413-416.
- Seifert, K. 1966. *Holz Roh-Werkst.* 24 (5): 185-189.
- Sharp, R. F. & H. W. O. Eggins. 1970. *Intern. Biodet. Bull.* 6 (2): 53-64.
- Sharp, R. F. & J. W. Millbank. 1973. *Experimentia* 29: 895-896.
- Shigo, A. L. 1965. *U.S. For. Serv. Res. Rep. NE-43*, 23 pp.
- Shigo, A. L. 1967. *Intern. Rev. For. Res.* 2, 237-299.
- Singh, S. & R. K. Tewari. 1970. *Indian For.* 96: 874-876.
- Smith, R. B., H. M. Craig & D. Chu. 1969. *Can. J. Bot.* 48: 1541-1551.
- Spaulding, P. & J. R. Hansborough. 1944. *U.S. Dep. Agric. Techn. Bull.* 876, 22 pp.
- Stalpers, J. A. 1978. *Studies in Mycol. No. 16*, CBS, Baarn, 248 pp.
- Stillwell, M. A. 1959. *For. Chron.* 35: 212-218.
- Thomas, G. P. & R. W. Thomas. 1954. *Can. J. Bot.* 32: 630-653.
- Ueyama, A. 1965. *Material Org. Beih.* 1, 325-332.
- Widden, P. & D. Parkinson. 1973. *Can. J. Bot.* 51: 2275-2290.
- Wilhelm, G. E. 1975. *Über den mikrobiellen Abbau der Rinde von Fagus sylvatica und Picea abies*. – Diss. Univ. Hamburg.
- Wolf, F. & W. Liese. 1977. *Holz Roh-Werkst.* 35: 53-57.